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Modelling coral reef habitat trajectories: Evaluation of an integrated timed automata and remote sensing approach

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ABSTRACT

The rapid degradation of many reefs worldwide calls for more effective monitoring and predictions of the trajectories of coral reef habitats as they cross cycles of disturbance and recovery. Current approaches include *in situ* monitoring, computer modelling, and remote sensing observations. We aimed to combine these three sources of information for Aboré Reef in New Caledonia by using: (1) a generic timed automata model of reef habitat trajectories, (2) two high spatial resolution multispectral images acquired before and after hurricane Erika in a 2-year interval (March, 2003), and (3) extensive field data on Aboré's benthic community structure. Field and remote sensing observations were used to verify model predictions of habitat evolution during the 2-year interval. We also tested whether a fairly generic model of habitat evolution can be used to flag local incorrect image change detection interpretation. The automaton manipulates objects such as states, transitions and clocks (transition times), and we found that it is possible, with expert knowledge, to describe complex habitat trajectories with this formalism. On Aboré Reef, we analyzed 22 heterogeneous polygons mapped before and after hurricane Erika using a 36 habitat typology. We examined 75 trajectories suggested by the before–after image classifications and critically reviewed the benefits of the combined timed automata model-image approach. The Aboré Reef case study confirms that this is a fruitful path to maximize the benefits of both tools, and minimize their respective drawbacks. However, we conclude that timed automata and remote sensing analysis need to be locally optimized to achieve useful results, and suggests further improvements by using hybrid models able to manipulate continuous, and fuzzy, properties.

1. Introduction

Countless environmental reports emphasize the degradation of coral reef habitats worldwide in the last 20 years (Hoegh-Guldberg, 1999; Lapointe, 1999; Porter et al., 2001). This situation is due to a variety of natural and anthropogenic causes. In coastal areas with dense human population, land-source pollution, land erosion, land reclamation have significantly altered coral reefs integrity. Overfishing and tourism activities also threat both the coastal and the most remote reefs. In addition, coral reefs are impacted periodically by natural catastrophes such as hurricanes, algal blooms, *Acanthaster planci* starfish infestations, diseases and coral bleaching. As a consequence, there are many examples of phase-shifts, where a reef dominated by coral becomes dominated by fleshy macroalgae.

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To understand habitat response to different reef stressors and effectiveness of management actions, it is necessary to monitor impact and recovery. The diagnosis can be complicated by repeated and convoluted multiple disturbances across time (Adjeroud et al., 2005; Ostrander et al., 2000). In addition, it is exceptional to have long-term *in situ* ecological data that could provide meaningful trends (*e.g.* Dustan and Halas, 1987; Done, 1992a, 1997; Tanner et al., 1996; Connell, 1979; Adjeroud et al., 2005). At best, time-series spanning 30 years are available for a few individual reefs, but these data still do not capture entire cycles of reef regeneration. Coral habitat recovery may need much more than 50 years to return to a climax state of high coral cover. The modern drastic habitat changes that we observe, and the paucity of long-term observations, have promoted the development of several generic models of coral habitat evolution, with a focus on coral community evolutions (*i.e.* strategy-shift from one dominant growth form to another) and phase-shits.

Decision-support tools explicitly attempt to predict successions of ecological states using a variety of mathematical tools, accounting for different type of stressors, *in situ* data and ecological assumptions (Tanner et al., 1996). They include a large variety of formalism, from generic qualitative models of reef habitat evolution (Done, 1999) to analytical dynamic models such as transition matrices models (Hughes, 1984; Done, 1987; Babcock and Davies, 1991). The goal is to forecast how critical system variables (*e.g.* coral cover) are most likely (*e.g.* quantified with probabilities) to change, in response to a given disturbance. Predicting ecological trajectories is complicated by the convolution of complex processes occurring at very different temporal and spatial scales. Thus, these models are generally limited to given ranges of time and space, and to a given suite of processes. For instance, Tanner et al. (1996) measured and modelled the effects of history on coral community dynamics for shallow reef crests of Heron Island (Australia). The community and habitat scales are probably the most difficult to handle because of the inherent variability in terms of environment, composition, architecture, history and responses to stress. Integrating the specificities of local habitats and communities is a major challenge when trying to model and predict the behavior of coral reefs facing disturbances (Marshall and Baird, 2000; Done et al., 2003). Several types of models have been used or are currently under development to predict coral reef habitat dynamics (including stage-based model, agent-based, Bayesian belief network) but several others still need to be explored.

Constructing models for the relevant time-space context requires descriptions of the different states of the system, the transitions between states, and eventually the full trajectory from an initial to a final state given a time period or cycles of coral loss/recovery. In a model, these transitions are triggered by some processes (short term disturbances, chronic disturbances, gradual recovery) and/or observational evidence. Then, a model needs to provide a mechanism to propagate the information to infer how the information at one step (assumed true by the model, by empirical knowledge, statistical correlations or by observations) can lead to another state. Uncertainties (*e.g.* probabilities for Bayesian networks), should be handled by the propagation process (Wooldridge et al., 2005). Therefore, a key aspect in the choice of a model is the formalism describing states and transitions, propagation process (*i.e.* combination of information) and, handling of time constraints. For instance, Lirman (2003) proposed a transition-matrix model with a 1-year step-time to predict the effects of storm intensity and frequency on Caribbean *Acropora palmata* populations. SIMREEF (Kudo and Yamano, 1997) is a finite-element model with a 1-month step-time that simulates coral cover variations for Ryukyus (Japan) reef communities made of six coral species. We have emphasized a general lack of good *in situ* ecological time-series data. However, many programs now routinely monitor reefs, and in 50 years, there should be plenty of long-term data. Because of logistical costs, though, these data may be spatially very limited, with a handful of sites per reef or reef complex. To overcome this spatial challenge, remote sensing is a logical solution (Andréfouët and Riegl, 2004). Remote sensing digital multispectral images are now routinely available at moderate cost and can be acquired following a given schedule or on-demand after a disturbance event (Elvidge et al., 2004). For many areas worldwide, archived black-and-white or color aerial analog photographs provide the only synoptic views of reefs before the impacts of modern disturbances. The utility of these long-term observations for change detection and habitat mapping has been well demonstrated (Yamano et al., 2000; Lewis, 2002; Cuevas-Jiménez et al., 2002; Andréfouët et al., 2001, 2005; Palandro et al., 2003). With such potential power at hand, it is critical to evaluate ecological models that are also able to integrate remote sensing data. Solutions immediately available are cellular automata (CA) and timed automata (TA) approaches which have been applied to urban sprawl, intertidal area dynamics and agriculture mapping and modelling (Liu and Phinn, 2003; Marchand and Cazoulat, 2003; Largouët and Cordier, 2000). CA are discrete dynamic systems made of agents (*i.e.* pixels) that change states over time according to the state of the neighbor-agents and a set of rules. This is a powerful image classification approach (Marchand and Cazoulat, 2003). CA have also been used to model the complex dynamics of coral colonies from different species within a reef habitat (Langmead and Sheppard, 2004). However, for inter-habitat relationships, there is little information available on how coral reef habitats affect the dynamics of other habitats at different spatial scales (cf. discussion in Purkis et al., 2005), much less how the dynamics could be represented with simple rules. Furthermore, an important model feature is the capacity to handle *uncertain* time constraints. When it is necessary to model the evolution of one agent according to external events with uncertainty on the time constraints, TA approaches sound appropriate. TA offers the capacity to easily inject qualitative expert knowledge and uncertain time constraints when describing the dynamics of a system (Largouët, 2000).

Our specific goals are thus to combine the power of TA formalism, remote sensing and compilation of *in situ* data to diagnose the status of a reef, track its history of disturbances and accurately map changes in habitat distribution. Our case study is Aboré Reef, New Caledonia, following the passage of Hurricane Erika in March 2003. Specifically, we test:

- if trajectories of reef habitats can be resolved using a suite of before–after event remote sensing images and a generic model of habitat evolution,

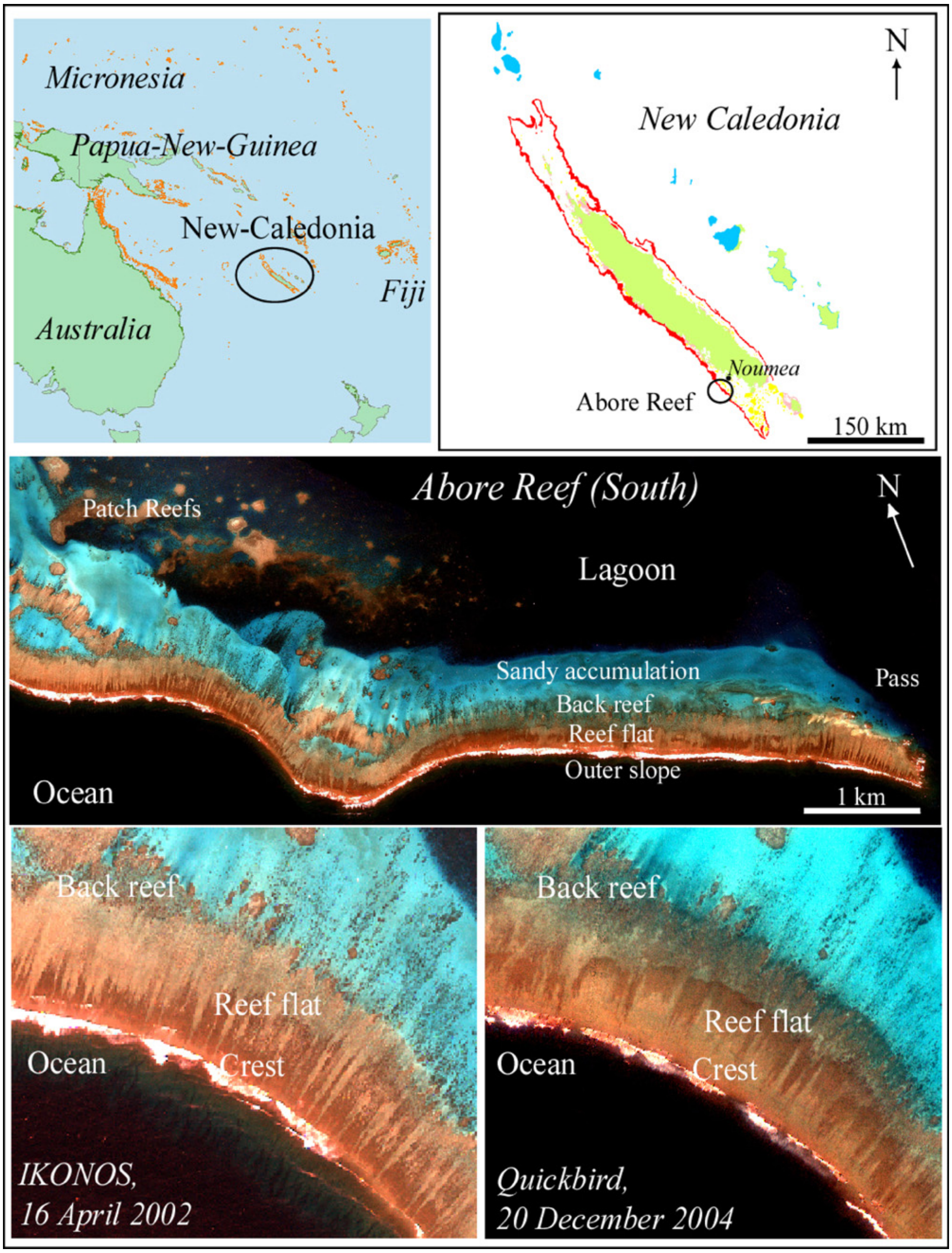

Fig. 1 – Upper-left: location of New Caledonia, among some of the largest reef systems worldwide (orange). Upper-right: Location of Aboré Reef among New Caledonia reef systems (red = barrier reef, blue: atolls and banks, yellow: lagoonal patch reefs, orange: fringing reefs). Middle: main geomorphological structures of Aboré Reef (IKONOS image). Bottom: enlargements of a section of Aboré Reef highlighting differences in benthic structures before and after Hurricane Erika (14th March 2003) using a IKONOS and a Quickbird images, respectively.

- if a generic model can help identify errors in image classification of habitat types.

2. Materials and methods

2.1. *Characterization of Aboré Reef habitats*

Aboré Reef is a 15-km long section of the barrier reef surrounding New Caledonia (Fig. 1), located 17 km westward of Noumea. Aboré is a marine protected area since 1981. This status and the proximity to Noumea have made Aboré Reef one of the most studied coral reefs in New Caledonia. The reef was impacted by the category 5 hurricane Erika on 14 March 2003; this was the first significant hurricane to strike this area since 1969 (Fig. 1). Coral bleaching occurred in western New Caledonia, however the effects have not been monitored and to the best of our knowledge no quantitative data exist to assess any subsequent mortalities (Richer de Forges and Garrigue, 1997). *A. planci* starfish predations on corals have also been

Table 1 – General hierarchical structure for habitat definition, and specific end-members of substratum and benthic cover

General geomorphology		Physical parameter	Substratum		Coral status	Benthic cover		
Level I	Level II		Hard	Soft		Live coral	Algae	Other
Fringing reef	Reef flat Forereef	Depth Topography[a]	Rock Pavement	Sand Rubble	Live Bleached	Tabular Massive	Turf Coralline	Sponges Soft coral
Lagoon	Lagoon	Complexity[b]	Old dead coral	Boulder	Recently dead	Sub-massive	Fleshy algae	Benthic invertebrates
Lagoon patch reef	Forereef Crest Reef flat			Small and large	Dead encrusted	Encrusting Open branching Foliose	Cyanobacteria Calcareous green algae	–
Barrier reef	Inner slope Back reef Reef flat Crest Outer slope					Digitate *Millepora* spp. Compact branching		
Oceanic patch reef	Forereef Reef flat							

Aboré Reef habitat were described and modelled as a triplet {geomorphology, substratum, benthic cover}.The study includes only “Barrier reef” and “Lagoon patch reef” geomorphological zones. The “others” cover category was not used for the model.

[a] Topography is defined as the average vertical relief.

[b] Complexity is defined as an index of rugosity.

observed in the past, with local infestations reported in mid-2004 in nearby reefs. Aboré Reef is not directly at risk from any anthropogenic impacts (*i.e.* pollution and sedimentation due to the distance from the coast and local currents; Douillet et al., 2001). Thus, diseases, overfishing, pollution and eutrophication were not considered, and the suite of disturbances considered for the model was limited to the hurricane, bleaching and *A. planci* outbreaks.

In this study, a coral reef habitat is an explicit hierarchical triplet of {*geomorphology*, *benthic cover*, *coral growth form*}. Aboré reef geomorphology is characterized by an outer slope (not considered here), a large shallow, hard-bottom reef flat where most of the hurricane-induced devastation occurred, a back reef area where the reef flat is fragmented and is gradually dominated by sediments, and a shallow (2–4 m deep) sandy accumulation area where some large isolated patch reefs occur (Fig. 1). We surveyed the reef flat, back reef and patch reefs. Between September 2004 and July 2005, 85 sites were surveyed to ground-truth habitat variables (cover and architecture) using a rapid-survey technique (Cros, 2005). The variables listed in Table 1 were recorded and provided the foundation for a local typology of reef habitats. Since the spatial resolution of our images (described below) ranged between 2.5 and 4 m, habitat description was performed for areas of 10 m × 10 m.

We did not have reliable (*i.e.* correctly geolocated) habitat information acquired *in situ* before Hurricane Erika. However, to ensure that the habitat typology defined by post-hurricane ground-truthing also represented the pre-hurricane situation, we collected data on areas obviously undamaged by the hurricane, as determined by comparison of before and after images of the reef and confirmed by field observations. In these areas, coral colonies were flourishing, without obvious breakages, recent mortalities and new sediment deposits, or they were obviously damaged well before the hurricane, with long-eroded colonies.

2.2. Principles of timed automata

Timed automata (TA) were first introduced by Alur and Dill (1994). TA theoretically allows modelling high complexity system by referring to a discrete event formalism able to combine individual automata into more complex designs (Alur and Dill, 1994). To our knowledge, TA have not been used to model natural processes, but only simplified, human-controlled processes such as agriculture management (Largouët, 2000; Hélias, 2003). An automaton is at least composed of three elements: a *state*, a *transition*, and a *clock*. A relevant feature for our ecological goals is that quantitative temporal information on the timing of events can be taken into account with the clocks. Formally, a TA can be seen as septuplets $\langle \mathcal{S}\mathcal{X}\mathcal{L}\mathcal{E}\mathcal{I} \rangle$ (Schnoebelen, 1999), where $\mathcal{S}$ is a finite set of states, with $\int_0$ as the initial state, $\mathcal{X}$ a finite set of clocks, $\mathcal{L}$ a finite set of labels, $\mathcal{E}$ a finite set of transitions, with each transition $\rceil$ as a septuplet ($\int$, $\updownarrow$, φ, δ, $\int'$) such that $\rceil$ connects the state $\int$ to the location $\int'$ on symbol $\updownarrow$. The enabling condition required for all clocks is described by φ. δ, element of $\mathcal{X}$, describes the set of clocks to be reset when the transition $\rceil$ is triggered. $\mathcal{I}$:$\mathcal{S} \rightarrow \Phi(\mathcal{X})$ maps each state $\int$ with a clock constraint, called an invariant.

In practice, an automaton can be visualized and implemented as in Fig. 2A. States are systematically identified by

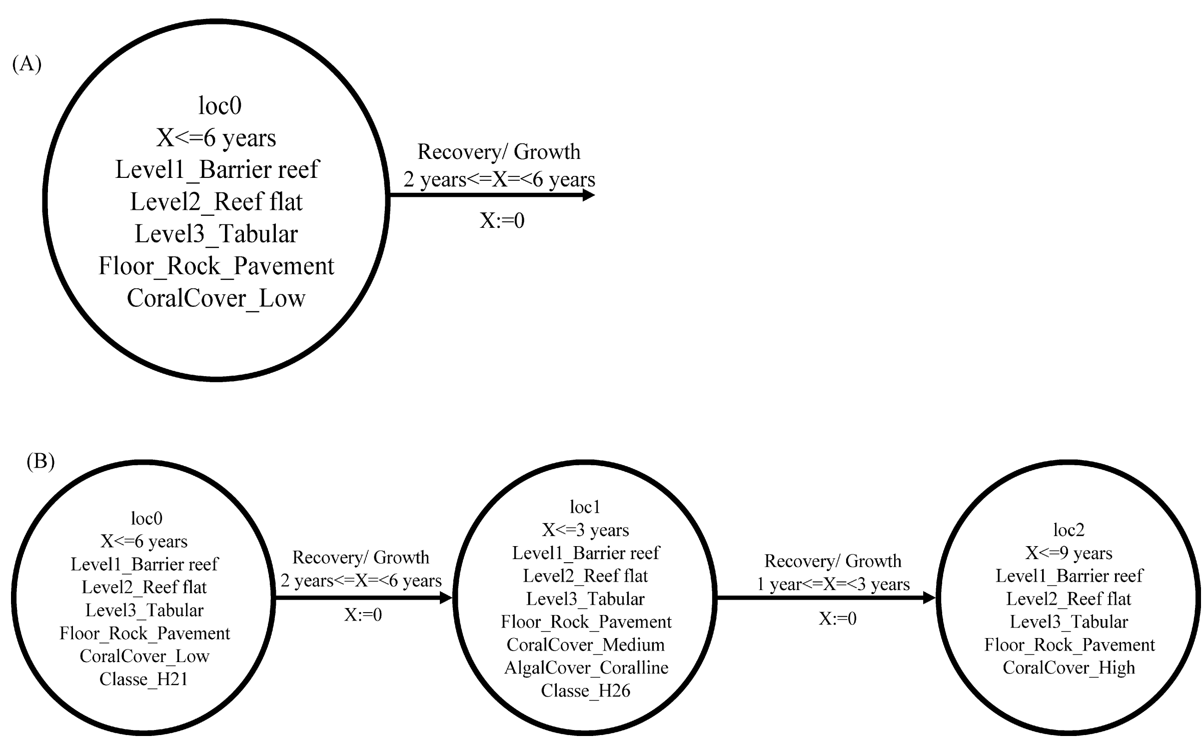

Fig. 2 – Principles and visualization of timed automata structure. (A) A state and its attributes and (B) transitions between states. Labels are in agreement with the actual model implemented for Aboré Reef.

a number (*e.g. loc0*) and described by an invariant (temporal constraint on the maximum duration of the state) and a set of properties (*e.g. Level1_Barrier reef* to *CoralCover_Low*). Each property has a label (*e.g. Level3_*) associated to a variable (*e.g. _Tabular* growth form) that can change from one state to another. A state can evolve to another state through the transitions. A *trajectory* is a sequence of transitions. A transition is systematically identified by a number, label, and is associated to a triggering condition, specified by the clock. A clock defines temporal constraints associated with a state and a transition. A clock can also be reset (X:=0) when a transition is triggered. X can be declared in any arbitrary units. One global clock synchronizes all event clocks. Several clocks are sometimes necessary to take into account independent time intervals. The unit step-time of the global clock is dependant on the application.

TA formalism allows construction of large models from independent sub-models composed of sub-automata constrained by the same time step (Schnoebelen, 1999). Several automata can be synchronized by particular events (called synchronized events), to obtain larger, composed, automata (Fig. 3).

Once a model has been built, it is necessary to test it. Different properties can be checked including *Reachability* (Schnoebelen, 1999). This word has been coined by TA specialists and is part of the TA vocabulary, thus we used it here. It is the most interesting property given our problem. In short, it describes if one state characterized by several intrinsic properties can be reached from another state, and through which trajectories. To run these checks, a model-checker is required. These are specific softwares useful to query the model properties and behavior, such as Kronos (Yovine, 1997) or UPPAAL (Larsen et al., 1997). The model-checker provides a simple binary diagnosis (*true* or *false*) whether the property is satisfied or not. If *reachability* is positive (*true*) the checker lists all the possible trajectories. A second check considers time and clocks. In this case, a *false* diagnostic means that no trajectory is possible in the time interval. A *true* diagnostic means that at least one trajectory is possible in the time interval. The model itself simply provides the set of possibilities without any type of ranking or sorting. More details on the timed automata formalism, model-checking techniques and types of queries can be found in Yovine (1997), Schnoebelen (1999), Largouët (2000) and references therein.

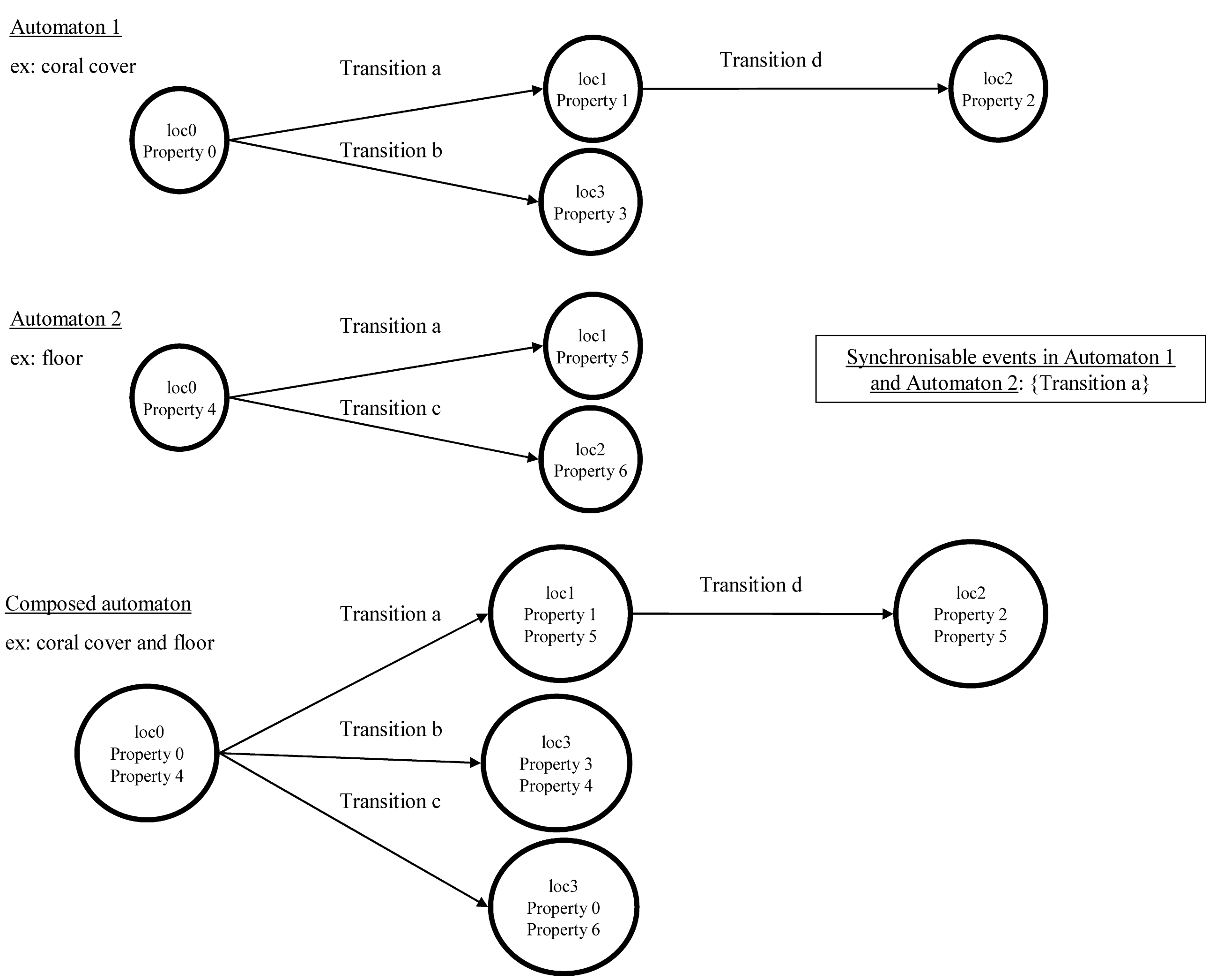

Fig. 3 – Principles of automata composition. The transition *a* common to two individuals automata 1 and 2 can be used to compose both automata into one single automaton.

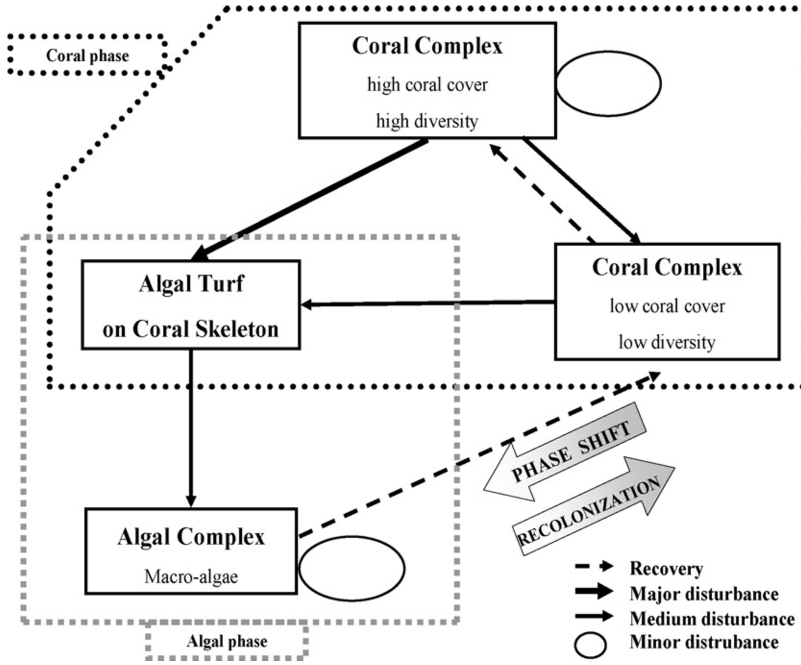

Fig. 4 – Separation between coral and algal phases. Phase-shift from coral dominance to fleshy algal dominance occurs through an ephemeral, reversible, state of turf colonizing coral skeleton.

2.3. *Model implementation*

2.3.1. *General temporal and spatial settings*

The objective is to generically describe coral reef habitat evolution at the decadal scale, from 1 to 50 years. We choose the 50-year threshold because it is the limit for most available airborne photographs. Moreover, this time interval allows inclusion of habitats able to regenerate one or several times, as well as habitats that do not regenerate once they have been impacted. Though the ultimate aim is a generic model of reef

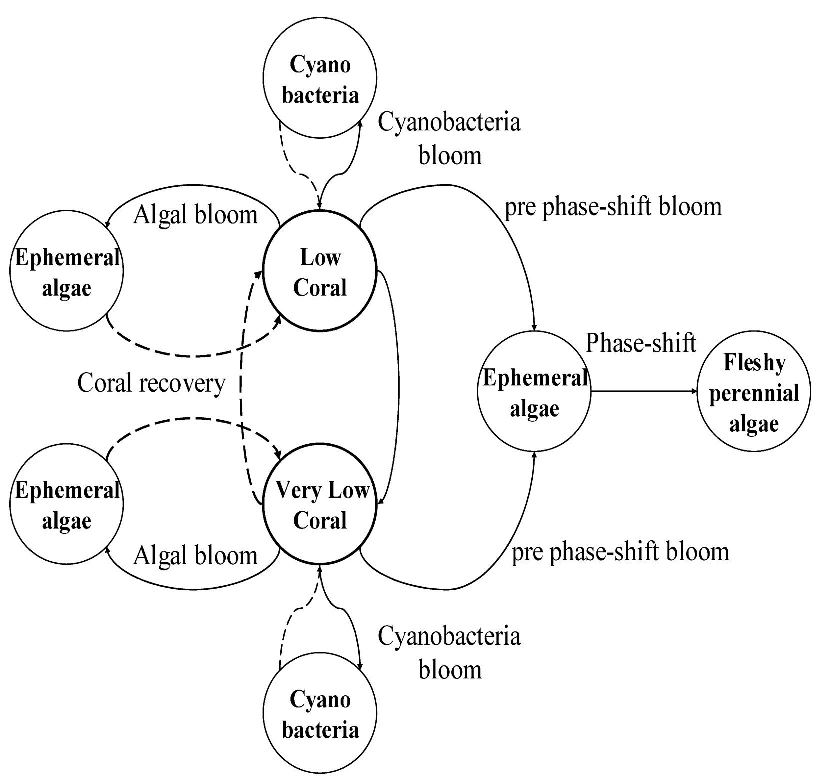

Fig. 5 – Detailed implementation of the ephemeral (turf or cyanobacteria) and permanent algal phase, from Low or Very Low coral cover states. "Bloom" implies significant increases in algae abundance and cover.

habitat evolution, it is currently unrealistic to target all habitats in all reefs worldwide in a single model. For instance *Acropora palmata* dominated habitats in the Caribbean have fairly specific states and transitions (Lirman, 2003). On the other hand, it is adequate to construct a model for a single reef, with specific structure, habitats and environmental forcing, that is representative of a range of reefs (*e.g.* inshore Caribbean fringing reef, or Indo-Pacific barrier reef). Aboré Reef shares many similarities with Indo-Pacific barrier and offshore reef systems. Thus, we parameterized necessary states, biological variables and clock setting (coral cover, growth, recovery rates, *etc.*) preferentially from available literature on Indo-Pacific barrier reefs and using experts' opinions.

2.3.2. *Ecological phases*

A coral reef system can maintain itself as a coral-dominated system, but can under a given suite of disturbances evolve into a new system, dominated by algae (Done, 1992b; Hughes, 1994; Diaz-Pulido and McCook, 2002) (Fig. 4). The model considered the algal phase as either a terminal transition to a

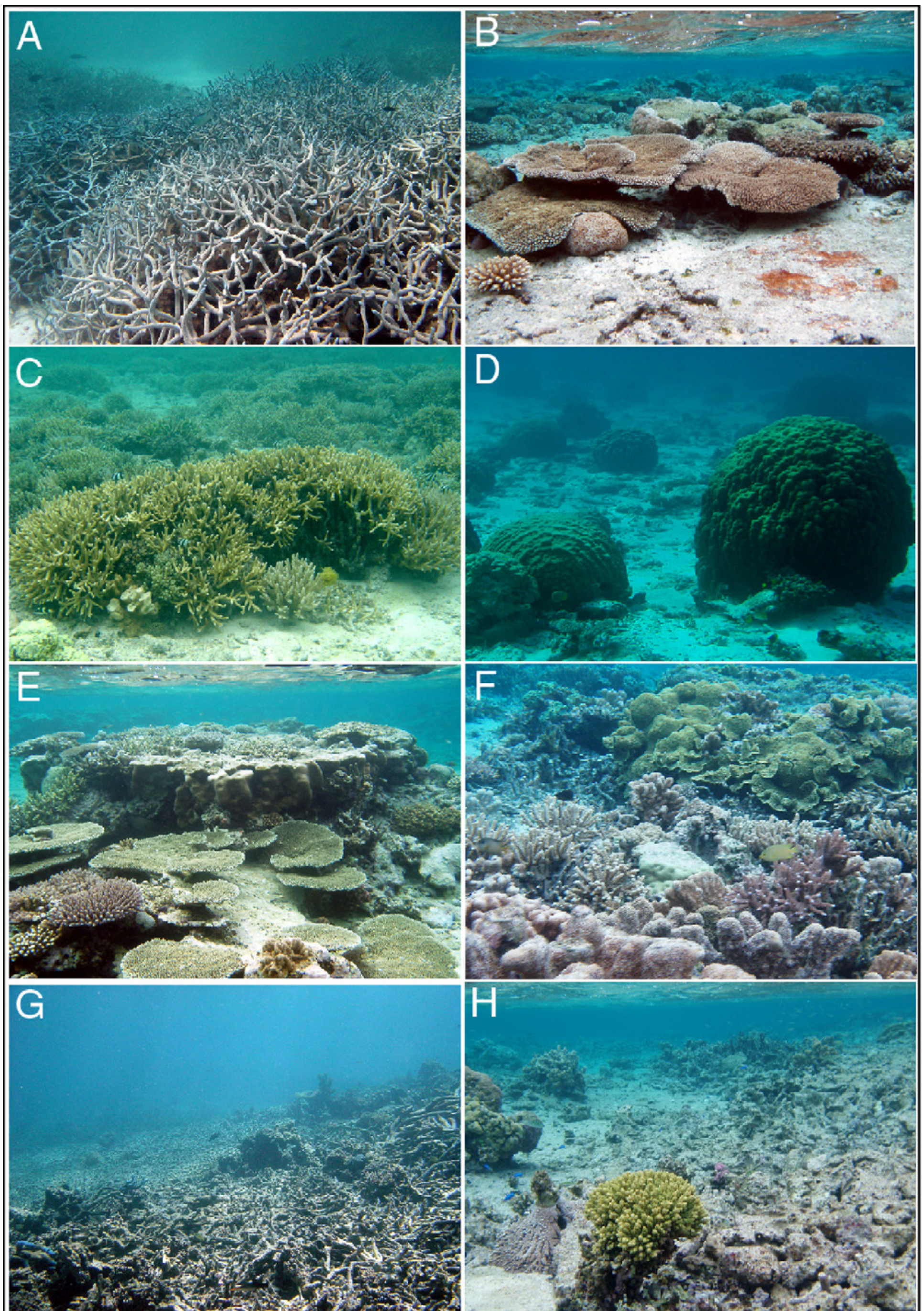

Fig. 6 – *In situ* photographs of Aboré Reef coral communities. (A) Open branching (high vertical development), (B) tabular, (C) compact branching (low vertical development), (D) massive, (E) and (F) mix communities, (G) post-hurricane facies with rubles, (H) post-hurricane facies with a visible limit of boulders and rubble deposit before coral colonies.

phase-shift or a temporary transition from which a coral community can recover. We included this phase-shift in the model, but not the dynamics of the algal system itself (Fig. 5) because this remains too poorly documented (Payri, 1987; Done, 1992b; Hughes, 1994; McClanahan and Muthiga, 1998; Stiger and Payri, 1999; McCook, 1999). In addition, algal phases were ephemeral on the reef crests Heron Reef (Australia), another offshore Indo-Pacifique reef (Tanner et al., 1996). Similarly, in all areas surveyed on Aboré Reef, we have not noticed any significant fleshy algae communities other than ephemeral cyanobacteria patches and limited areas covered by algal turfs. Encrusting coralline algae is the dominant flora throughout the reef flat. Thus, we included in the model only a systematic transition from the algal-dominated to coral-dominated phase. Cyanobacteria blooms were not considered as shifts towards the algal phase, but as temporary situations.

2.3.3. *Automaton structure: coral communities, coral cover and substratum automata and their composition*

We categorized five main coral communities from our surveys: tabular, massive, compact branching, open branching and mixed composition (Fig. 6). According to many studies worldwide, each has its own response to different stressors (Loya et al., 2001; De'ath and Moran, 1998; Massel and Done, 1993; Hughes, 1994; Augustin et al., 1997; Adjeroud et al., 2005), though the differences in recovery remain poorly documented (Andres and Rodenhouse, 1993; Connell, 1979; Done, 1992a, 1987). The model is built to allow strategy-shifts, *i.e.* shifts from one coral community to another. For instance, a completely dead tabular community can be recolonized by compact branching colonies. One exception, modelled in a specific way, is the soft-bottom open branching community of the barrier reef inner slope. This soft-bottom floor prevents strategy-shift from, or towards, an open branching community.

Table 2 – Classes of coral cover

Live coral percentage cover	Qualitative intervals for coral cover automata
[50;100[	Climax
[25;50[	High
[10;25[	Medium
[2;10[	Low
[0;2[	Very Low

We take advantage of the possibility to combine individual TA into larger ones using synchronized events. Here, we have considered two automata. The first automaton describes trajectories of coral cover, regardless of the type of coral community (Fig. 7). Since TA handle discrete events and data only, coral cover has been categorized into five qualitative categories (very low, low, medium, high and climax), corresponding to a range of percentage cover (Table 2). Shifts from one state to another depends recruitment and growth (*i.e.* recovery) and disturbance occurrences (massive or local bleaching events, hurricanes, or *Acanthaster* outbreaks). Different events affect coral cover with different strengths; for instance, a category 5 hurricane unconditionally decreases coral cover to the Very Low level, whereas a bleaching event can have a less serious effect.

The second automaton describes trajectories for substratum which can be altered depending on different processes and disturbances (*e.g.* Hughes and Connell, 1999) (Fig. 8). For example, physical destruction brought by a hurricane reduces coral colonies to fragments, removes the reef matrix and instantly introduces rubble and boulders to the system (Hubbard, 1992; Scoffin, 1993). Unconsolidated rubble can be cemented by coralline algae to form a new pavement after several years or decades, creating new space for recruitment and recovery (Macintyre et al., 2001).

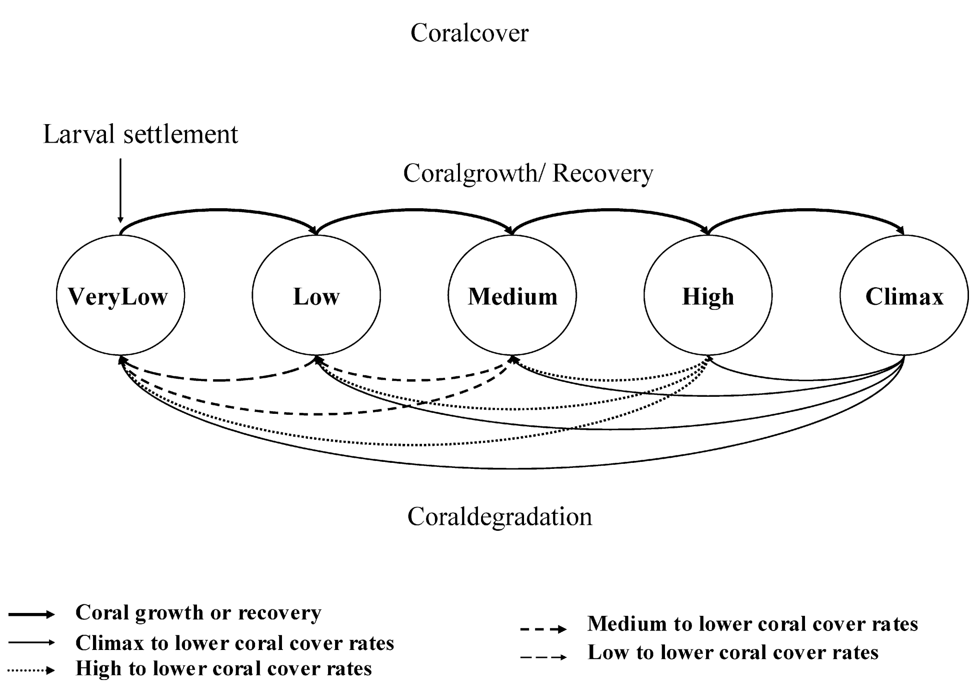

Fig. 7 – Basic structure of the timed automaton describing coral cover evolution.

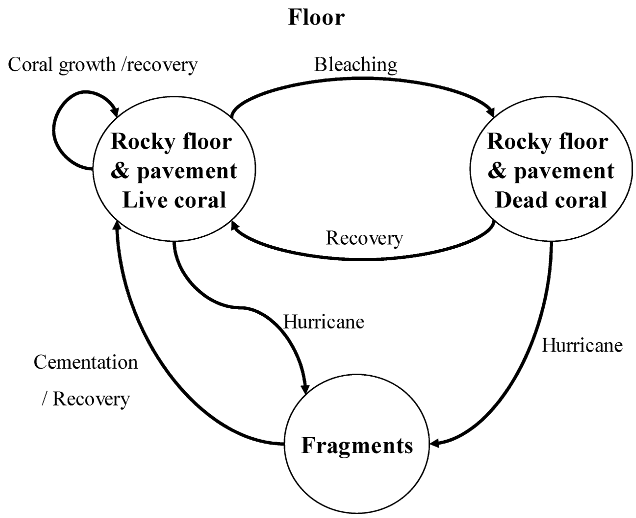

Fig. 8 – Basic structure of the timed automaton describing floor evolution.

We have made several assumptions for the combination of the two TAs. First, we assume that coral recovery cannot occur on mobile rubbles and boulders, but only after their cementation. Second, we assumed local deposition or limited transport, or in other words, we assumed that each coral community generates its own rubble. As such, boulders frequently encountered along the crest originating on the outer slope cannot be modelled at this stage. A third assumption is that bleaching events and *Acanthaster* outbreaks do not affect the substratum whereas hurricanes do (Loya et al., 2001; Hubbard, 1992; Scoffin, 1993; Massel and Done, 1993; Rogers, 1993; Hughes, 1999; Russ and McCook, 1999; Lirman, 2003). Considering the five coral communities we have defined for Aboré Reef, the final TA architecture consists of five different TA composed with one substratum TA (example for the Tabular community Fig. 9). In addition, based on the strategy-shifts which define possible transitions between four different coral communities (open branching community excepted), the four TA (tabular, compact branching, massive and mix communities) were composed within a larger automaton by these strategy-shift transitions (Fig. 10). A strategy-shift occurs if there is a transition from a Very Low cover of one growth-form type to a Low cover in another growth-form type. We specified a Very Low to Low threshold to consider the minimum gap showing a clear change (thus not Very Low to Very Low) and to minimize the time interval (thus not Very Low to Medium or higher).

To finalize the TA, we added the transitions toward ephemeral algal stages (turf, cyanobacteria) (Fig. 10). This stage can lead to a phase-shift (Augustin et al., 1997; River and Edmunds, 2001; McClanahan et al., 2001; Birrell et al., 2005). A phase-shift to a fleshy-algae-dominated habitat is considered here as a terminal stage. The transitions towards ephemeral or permanent algal cover occur when coral cover is Low or Very Low, and for pavement, rocky and mixed substrata. This shift is included here because of its relevance to reef ecology and to illustrate a possible model implementation of this transition; however, such a phase-shift did not occur on Aboré Reef.

2.3.4. *Clock setting*

We have implemented clocks based on the shortest relevant time interval, which is 1 day, *i.e.* the time required for a hurricane to destroy coral cover on a reef. A 1-week interval could have been also suitable. Each transition triggered by a hurricane, bleaching, *Acanthaster* infestation, recovery (one coral cover state to another), phase-shift and strategy-shift have been timed given a variety of reports from which we have derived most likely time-intervals (see ecology references throughout Section 2.3 and Table 3). In many instances, the information provided by the literature or by experts (personal communication) were not consistent, revealing the heterogeneity in spatial, temporal and ecological scales considered by each study. Therefore, we assigned average values with regular intervals in units of month or year (Table 3).

2.4. *An example of automaton*

We illustrate the model with one example. Fig. 2B illustrated a trajectory towards climax without disturbances for reef zone dominated by tabular corals, with an initial Low coral cover on a rock and pavement substratum that leads to a state *loc2* of High coral cover. The same tabular colony type in states *loc0* and *loc1* can be impacted by hurricanes, bleaching or *Acanthaster* outbreaks (Fig. 9). The hurricane reduces coral cover to Very Low and generates rubble and boulders. This defines a *loc3* state. A hurricane is an instantaneous event, occurring in 1 day ($X = 1$d), which is the time step for all further events. We assumed that a minimum of Medium coral cover is required to allow a massive *Acanthaster* outbreak to occur (Fig. 9). We also assumed in this example that the outbreak is a massive disturbance, bringing live coral cover to the lowest ranks, but with different time intervals for different coral types. This is *loc4* state (Fig. 9). The initial substratum attributes are not affected, but dead coral is now present. The higher the initial coral cover, the longer the starfish infestations. Fig. 9 also illustrates the responses of the system to a bleaching event. Coral cover decreases with bleaching. If bleaching strikes state *loc2*, the transition leads to *loc0*. Finally, Fig. 10 provides a more complete view of possible habitat dynamics, with the addition of cementation, ephemeral algal blooms, and phase-shift processes, thus new states, transitions and clocks.

2.5. *Interface between image and model*

In Figs. 2, 9 and 10, the state includes a property labelled "*Habitat_*". This property links all states to a typology of habitats which depend on remote sensing habitat map classification (Section 2.6). This property makes the connection explicit between timed automata and remote sensing in our model of habitat evolution.

2.6. *Remote sensing data and image processing*

The suitability of the model to characterize reef habitat transition and detect image classification errors was tested with a pair of very high-resolution images, acquired before and after Hurricane Erika. These were an IKONOS image (4 m spatial resolution) acquired 16 April 2002 and a Quickbird image (2.5 m resolution) acquired 20 December 2004 (Fig. 1). Both images

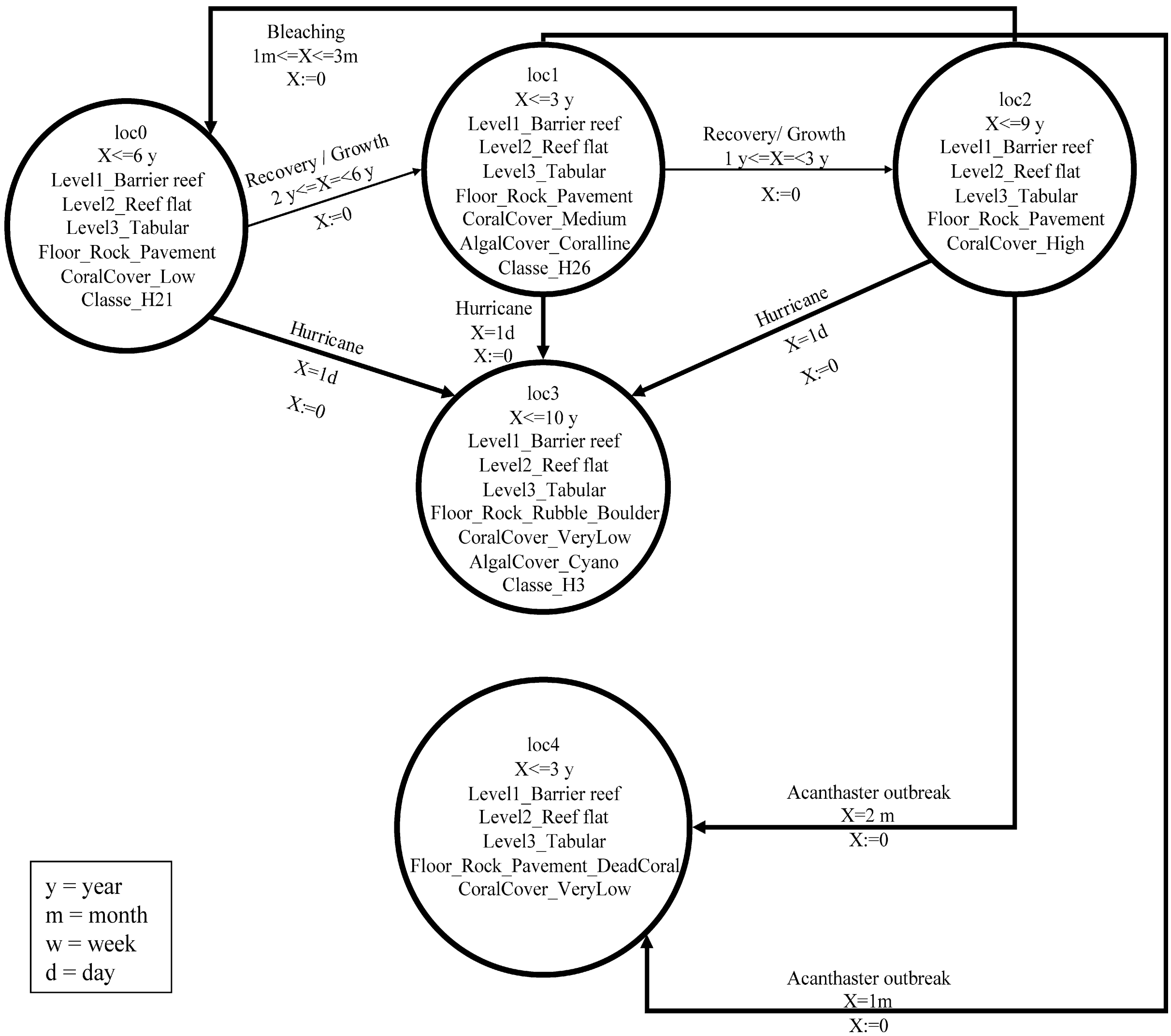

Fig. 9 – Example of model of evolution for a tabular coral community submitted to three disturbances: hurricane, *Acanthaster* outbreak and bleaching. Clocks (*X*) are shown for clarity in days (d) and years (y) but the time step unit is the day (cf. Section 2).

were multispectral, with three visible wavebands – blue, green and red – useful for this study. Both images were provided in UTM WGS 84 geodetic projection with excellent accuracy well within these sensors' theoretical specifications (±12 m horizontal accuracy). Geometric and radiometric correction were performed image-to-image using the Quickbird image as a reference (Andréfouët et al., 2001; Song et al., 2001).

Since the goal is to test the model by providing it as many scenarios as possible, we followed an original habitat mapping procedure. On purpose, our model includes a highly complex typology of habitats with 36 classes, which were mapped by supervised classification on both images before and after hurricane Erika regardless of their geomorphological setting (Section 3). Considering 36 classes was obviously unreasonable with respect to map accuracy, but reflected the full complexity of habitats that we found after the field surveys (*i.e.* all existing combinations of substratum and growth form habitat variables). A total of 36 classes would generate numerous image classification errors but also many unlikely habitat transitions that the model should be able to detect. Conversely, several transitions should be realistic and the model should confirm their reachability, within the actual time interval (*i.e.* 2 years) between the before–after images.

To test the model, there was no need to test every pixel on the image, which would have requested prohibitive computer time. In addition, working at pixel level is difficult, almost impossible, because images are not absolutely perfectly georeferenced. An approach per clusters of pixels capturing a range of habitats is much safer. Thus, we defined 22 representative polygons in different areas of the reef that covered areas both untouched and heavily impacted by the hurricane. All polygons were spatially independent of the 85 training sites used to define the spectral statistics for each of the 36 habitat classes and to define the habitat typology. Most polygons were fairly homogeneous, but several included a variety of habitats, but never more than four.

The pixels within each of these test-polygons (ranging in size from 60 to 1400 pixels) were classified using the Mini-

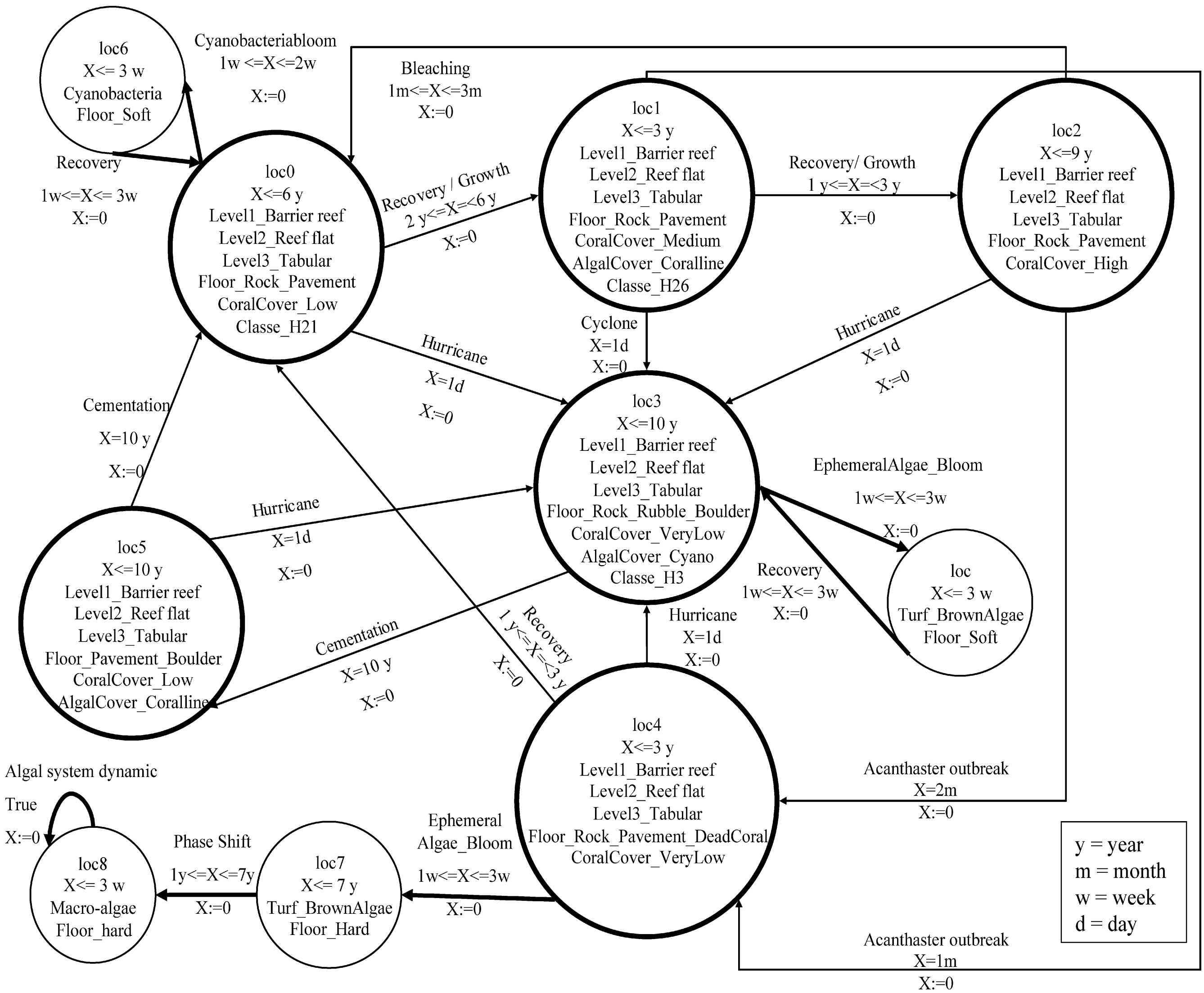

Fig. 10 – Example of model of evolution for a tabular coral community submitted to three disturbances: hurricane, *Acanthaster* outbreak and bleaching, plus possible transitions towards phase-shifts. Clocks (*X*) are shown for clarity in days (d), months (m) and years (y) but the time step unit is the day (cf. Section 2).

mum Distance supervised classification scheme available in the ENVI® image processing toolbox. After classification, for each polygon, we computed the frequencies of occurrence of the 36 habitat classes. We considered that this frequency corresponded to the probability that the class was present in the polygon (Matsakis et al., 2000). The class frequency histograms were thresholded following two empirical rules. First, given our ground-truth data, no more than four classes could be present within one polygon, thus only the four highest probabilities were considered. Second, if one of these four classes had a low probability (<10–15%), it was discarded, and we kept only the classes above these thresholds. Thus, each polygon provided one to four highly probable habitat classes based on radiometric properties and classification. By performing this analysis on both images before and after Hurricane Erika, we obtained two distributions of habitat classes, 2-years apart, for each of the 22 polygons.

2.7. *Model testing*

For each polygon, we obtained from the image classifications a series of one to four possible habitat classes both before and after the hurricane. For each combination of before–after habitat classes, the model was queried by testing the reachability as explained above, first without time constraints, then with time constraints.

3. Results

3.1. *Field observations and typology of habitats*

Ground-truth identified 36 habitat classes on Aboré Reef (Table 4). Two were obviously the results of Hurricane Erika: vast expanses of rubble fields and relics of compact branch-

Table 3 – Clock settings for transitions between coral cover states (VL: Very Low; L: Low; M: Medium, H: High, C: Climax) for different types of events, and for the different coral communities (CB: Compact branch form; Tab: Tabular form; Mi: Mix composition; Ma: Massive form)

		Compact branch	Tabular	Massive	Mix composition	Open branch	References
Local bleaching	C to L	1–3 months	1–3 months	6 months	4–5 months	1–3 months	McClanahan et al. (2001), Mumby et al. (2001), De'ath and Moran (1998), Augustin et al. (1997), Dollar and Tribble (1993), Gleason (1993)
	H to L	1–3 months	1–3 months	6 months	4–5 months	1–3 months	
	M to L	1–3 months	1–3 months	6 months	4–5 months	1–3 months	
Global bleaching	C to L	1–3 months	1–3 months	6 months	4–5 months	1–3 months	
	H to L	1–3 months	1–3 months	6 months	4–5 months	1–3 months	
	M to L	1–3 months	1–3 months	6 months	4–5 months	1–3 months	
Acanthaster	C to VL	6 months	6 months				Brown (1997), Augustin et al. (1997), Done (1987), Chabanet (personal communication, 2005)
	C to M			6 months	5 months		
	H to VL	2 months	2 months				
	H to M				1 month		
	M to VL	1 month	1 month	5 months			
	M to VL[a]			2 months			
Cyclone	1 day	1 day	1 day	1 day	1 day		
Recovery	VL to L	1–3 years	1–3 years	1–3 years	2–6 years	1–3 years	Augustin et al. (1997), Hughes (1994), Gleason (1993), Done (1992b), Adjeroud (personal communication, 2005)
	L to M	2–6 years	1–3 years	6–18 years	2–6 years	1–3 years	
	M to H	1–3 years	1–3 years	4–12 years	2–6 years	1–3 years	
	H to C	3–9 years	2–5 years	15–45 years	1–3 years	2–5 years	
Bloom Turf	1–3 weeks	1–3 weeks	1–3 weeks	1–3 weeks			Payri (personal communication, 2005)
Bloom Cyano	2 weeks to 2 months	2 weeks to 2 months	2 weeks to 2 months	2 weeks to 2 months			Golubic (personal communication, 2005)
Bloom Turf pre-phase-shift	1–4 weeks	1–4 weeks	1–4 weeks	1–4 weeks			Payri (personal communication, 2005)
Phase-shift	1–7 years	1–7 years	1–7 years	1–7 years			Obura (2005), McClanahan et al. (2001), McClanahan and Muthiga (1998), Augustin et al. (1997), Gleason (1993), Done (1992b), Payri (personal communication, 2005)
Strategy-shift (VL to L)	CB to Tab	1–3 years					Dollar and Tribble (1993), Adjeroud (personal communication, 2005), Chabanet (personal communication, 2005), Baird (personal communication, 2005)
	CB to Mi	2–6 years					
	Tab to CB		1–3 years				
	Tab to Mi		2–6 years				
	Tab to Ma		6–18 years				
	Ma to Mi			2–6 years			
	Ma to Tab			1–3 years			
	Mi to Ma				< 1 year		
	Mi to Tab				1–3 years		
	Mi to CB				1–3 years		

[a] Eroded coral. Other references are mentioned throughout Section 2.3.

Table 4 – Main characteristics of habitat classes

ID habitat	Geomorphology	Floor	Coral community	Coral cover	Coral cover category	Algae
H1	Back reef	Rock	Mix	10	Medium	Coralline
H2	Back reef	Rock, dead coral	–	0	Very Low	Turf
H3	Back reef	Rubble	–	0	Very Low	Cyano
H4	Back reef	Rubble	Massive	5	Low	Coralline
H5	Back reef	Heterogeneous	Mix	15	Medium	Coralline
H6	Back reef	Pavement	Mix	25	High	Coralline
H7	Back reef	Rubble	Mix	25	High	Cyano
H8	Crest	Boulder	–	0	Very Low	Turf
H9	Crest	Boulder	–	0	Very Low	Coralline
H10	Crest	Dead coral	Compact Br	2	Very Low	Turf
H11	Crest	Pavement	–	0	Very Low	Coralline
H12	Crest	Rock	Compact Br	80	Climax	Coralline
H13	Crest	Rock, dead coral	–	0	Very Low	Turf
H14	Crest	Rubble	–	0	Very Low	Coralline
H15	Crest	Rubble, Pavement	–	0	Very Low	Coralline
H16	Lagoon	Sand	Open Br	50	Climax	Turf
H17	Pass	Rock	Massive	80	Climax	Coralline
H18	Pass	Rock	Mix	50	Climax	Coralline
H19	Patch crest	Pavement	Compact Br	35	High	Coralline
H20	Patch crest	Rock	Tabular	50	Climax	Coralline
H21	Patch reef flat	Pavement	Tabular	5	Low	Coralline
H22	Patch reef flat	Rock	Compact Br	10	Medium	Coralline
H23	Patch reef flat	Rock	Compact Br	80	Climax	Coralline
H24	Patch reef flat	Rock	Mix	5	Low	Coralline
H25	Patch reef flat	Rock	Mix	10	Medium	Coralline
H26	Reef flat	Pavement	Tabular	15	Medium	Coralline
H27	Reef flat	Rock	Mix	10	Medium	Coralline
H28	Reef flat	Rock	Mix	15	Medium	Coralline
H29	Reef flat	Rubble	–	0	Very Low	Turf
H30	Sandy accumulation	Rubble, sand	–	0	Very Low	Cyano
H31	Sandy accumulation	Sand	–	0	Very Low	Cyano
H32	Sandy accumulation	Sand	–	0	Very Low	–
H33	Sandy accumulation	Sand	Open Br	1	Very Low	–
H34	Sandy accumulation	Sand	Open Br	15	Medium	Turf
H35	Sandy accumulation	Sand	Open Br	30	High	Turf
H36	Sandy accumulation	Sand	Open Br	80	Climax	Turf

Coral cover categories are defined in Table 2. Br: branch.

ing field close to the crest (Fig. 6). Other areas were clearly non-impacted with High or Very High coral cover and large colonies. Finally, the third type of habitat included areas previously impacted by some type of disturbances, but not Erika. This included inner, sheltered sections of the reef flat and back reef, with dead standing branching and tabular colonies covered by algal turf, and no rubble on the substratum. There was a wide range of coral cover, from Very Low to Very High, for most coral community types. Cyanobacteria mats were present at the limit of the reef flat and back-reef sandy accumulation, and over some back-reef rubble fields. Rubble field types included recent deposits of fine branching coral debris, and coarser debris and boulders close to the crest. Eroded floors covered by coralline algae were frequent. On these rocky substrates, coral cover was generally Very Low to Medium. Massive colonies of several meters in diameter were encountered on the back reef and pass areas, and also in basins close to the crest. *Porites* spp. micro-atolls and coalescent colonies occurred on the back reef. These massive colonies appeared healthy, but isolated in expanses of rubble in some areas. Isolated tabular colonies were frequently dominant on smooth pavement susbtratum areas, while mixed communities favored more rugose susbtratum. Thickets of open branching colonies (*e.g. Acropora grandis*) were found on back reef and sandy accumulation areas, and sand pools enclosed in the reef flat. Habitats on reef flats and patches were similar, and we did not try to separate them further in the analysis based on geomorphology attributes. Only benthic cover and coral growth forms were used for the model without further distinction between geomorphological strata.

3.2. *Trajectory analysis: general trends*

The classification in 36 habitats of the 22 polygons provided the before and after matrices of habitat occurrences (Figs. 11 and 12). Several habitats dominated by rubble were correctly never found in the before-hurricane polygons. Table 5 (columns 7–12) provides results of the model queries for each polygon, without and with time constraints. For illustration purposes, we detail results for Polygon 11. Polygon 11 was classified as habitat H12 (rocky floor with a compact branching coral community, Climax live cover) by the before-hurricane image classification, and as H29 (rubble) and H9 (boulder) by the after-hurricane image classification. Thus,

Table 5 – Results of trajectory analysis for 19 polygons out of 22 (not shown are polygons providing only discarded "false" unrealistic trajectories, see text)

Polygon	Before	After	Reachability test						Temporal test
			Trajectory	True/false	Nb trajectory	First transition			
						Name	Clock (days)	Nb trajectory	2 years
P1	H31	H31	H31–H31	True	1				True
	H34	H18	H31–H18	False					
			H34–H31	False					
			H34–H18	False					
P2	H35	H35	H35–H35	True	1				True
	H34	H34	H35–H34	False					
			H34–H35	True	9	Massive bleaching	$30 \leq X \leq 90$	4	True
						Bleaching	$30 \leq X \leq 90$	3	True
						Hurricane	$X = 1$	1	True
						Recovery	$365 \leq X \leq 1095$	1	True
			H34–H34	True	1				
P3	H21	H21	H21–H21	True	1				True
	H25	H25	H21–H25	True	>18,000	Bleaching	$30 \leq X \leq 90$	N/A	False
	H1					Hurricane	$X = 1$	N/A	False
						Recovery	$730 \leq X \leq 2190$	N/A	False
						Cementation	$X = 3650$	N/A	False
			H25–H21	True	570	Massive bleaching	$120 \leq X \leq 150$	113	False
						Hurricane	$X = 1$	18	False
						Recovery	$730 \leq X \leq 2190$	439	False
			H25–H25	True	1				
			H1–H21	True	570	Massive bleaching	$120 \leq X \leq 150$	113	False
						Hurricane	$X = 1$	18	False
						Recovery	$730 \leq X \leq 2190$	439	False
			H1–H25	True	1				True
P4	H7	H7	H7–H7	True	1				True
	H6	H30	H7–H30	False					
			H6–H7	True	20	Local bleaching	$120 \leq X \leq 150$	3	False
						Massive bleaching	$120 \leq X \leq 150$	3	False
						COT outbreak	$X = 30$	3	True
						Hurricane	$X = 1$	1	True
						Recovery	$2555 \leq X \leq 7665$	10	False
			H6–H30	False					
P5	H8	H8	H8–H8	True	1				True
	H9	H23	H8–H23	False					
	H12	H4	H8–H4	False					
			H9–H23	False					
			H9–H4	False					
			H12–H8	False					
			H12–H23	True	1				True
			H12–H4	False					
P6	H18	H18	H18–H18	True	1				True
	H21	H22	H18–H22	True	>4,000	Local bleaching	$120 \leq X \leq 150$	N/A	False
						Massive bleaching	$120 \leq X \leq 150$	N/A	False
						COT outbreak	$X = 150$	N/A	False
						Hurricane	$X = 1$	N/A	False
			H21–H18	False					
			H21–H22	True	592	Local bleaching	$30 \leq X \leq 90$	132	False
						Hurricane	$X = 1$	110	False
						Recovery	$730 \leq X \leq 2190$	230	False
						Cementation	$X = 3650$	120	False
P7	H31	H34	H31–H34	True	1	Recovery	$365 \leq X \leq 1095$	1	True
	H16	H32	H16–H34	False					
	H33		H33–H34	True	1	Recovery	$365 \leq X \leq 1095$	1	True
			H31–H32	False					
			H16–H32	False					
			H33–H32	False					

Table 5 (*Continued*)

Polygon	Before	After	Reachability test						Temporal test
			Trajectory	True/ false	Nb trajectory	First transition			
						Name	Clock (days)	Nb trajectory	2 years
P8	H7	H34	H7–H34	False					
	H5	H5	H7–H5	False					
			H5–H34	False					
			H5–H5	True	1				True
P11	H12	H29	H12–H29	True	17	Local bleaching	$30 \le X \le 90$	8	True
		H9				Massive bleaching	$30 \le X \le 90$	4	True
						COT outbreak	$X = 60$	4	True
						Hurricane	$X = 1$	1	True
			H12–H9	True	17	Local bleaching	$30 \le X \le 90$	8	True
						Massive bleaching	$30 \le X \le 90$	4	True
						COT outbreak	$X = 60$	4	True
						Hurricane	$X = 1$	1	True
P12	H18	H4	H18–H4	False					
		H2	H18–H22	True	25	Local bleaching	$120 \le X \le 150$	8	True
						Massive bleaching	$120 \le X \le 150$	1	True
						COT outbreak	$X = 150$	8	True
						Hurricane	$X = 1$	8	True
P13	H7	H7	H7–H7	True	1				True
		H3	H7–H3	True	614	Recovery	$730 \le X \le 2190$	572	False
						Massive bleaching	$120 \le X \le 150$	21	False
						Hurricane	$X = 1$	21	False
P14	H12	H25	H12–H25	True	>5,000	Recovery	$365 \le X \le 1095$	?	False
	H23	H29				Hurricane	$X = 1$	?	False
		H14	H12–H29	True	17	Local bleaching	$30 \le X \le 90$	8	True
						Massive bleaching	$30 \le X \le 90$	8	True
						Hurricane	$X = 1$	1	True
			H12–H14	False					
			H23–H25	True	>5,000	Local bleaching/ massive bleaching	$30 \le X \le 90$	N/A	False
						COT outbreak	$X = 180$	N/A	False
						Hurricane	$X = 1$	N/A	False
			H23–H29	True	>7,000	Local bleaching/ massive bleaching	$30 \le X \le 90$	N/A	True
						COT outbreak	$X = 180$	N/A	True
						Hurricane	$X = 1$	N/A	True
			H23–H14	False					
P15	H5	H5	H5–H5	True	1				True
	H24	H1	H5–H1	True	3	Recovery	$730 \le X \le 2190$	1	False
	H33					Massive bleaching	$120 \le X \le 150$	1	True
						Hurricane	$X = 1$	1	True
			H24–H5	True	1	Recovery	$730 \le X \le 2190$	1	False
			H24–H1	True	2	Recovery	$730 \le X \le 2190$	2	False
			H33–H5	False					
			H33–H1	False					
P16	H23	H2	H23–H2	True	>12,000	N/A	N/A	N/A	True
		H13	H23–H13	True	959	Local bleaching	$30 \le X \le 90$	15	True
						Massive bleaching	$30 \le X \le 90$	1	True
						COT outbreak	$X = 180$	1	True
						Hurricane	$X = 1$	942	True
P17	H2	H2	H2–H2	True	1				
	H23		H23–H2	True	>12,000	N/A	N/A	N/A	True
P18	H18	H18	H18–H18	True	1				True
	H12		H12–H18	True	>1,700	Local bleaching/ massive bleaching/COT outbreak	$30 \le X \le 90$	N/A	False
						Hurricane	$X = 1$	N/A	False

Table 5 (Continued)

Polygon	Before	After	Reachability test						Temporal test
			Trajectory	True/ false	Nb trajectory	First transition			
						Name	Clock (days)	Nb trajectory	2 years
P20	H5	H3	H5–H3	True	614	Recovery	$730 \le X \le 2190$	572	False
	H7					Massive bleaching	$120 \le X \le 150$	21	False
						Hurricane	$X = 1$	21	False
			H7–H3	True	614	Recovery	$730 \le X \le 2190$	572	False
						Massive bleaching	$120 \le X \le 150$	21	False
						Hurricane	$X = 1$	21	False
P21	H16	H20	H16–H20	False					
	H19	H16	H16–H16	True	1				True
	H20		H19–H20	True	1,220	Local bleaching	$30 \le X \le 90$	255	False
						Massive bleaching	$30 \le X \le 90$	152	False
						COT outbreak	$X = 60$	152	False
						Hurricane	$X = 1$	50	False
						Recovery	$1095 \le X \le 3295$	611	False
			H19–H16	False					
			H20–H20	True	1				
			H20–H16	False					
P22	H23	H10	H23–H10	True	959	Local bleaching	$30 \le X \le 90$	15	True
		H23				Massive bleaching	$30 \le X \le 90$	1	True
						COT outbreak	$X = 180$	1	True
						Hurricane	$X = 1$	942	True
			H23–H23	True	1				True

COT; crown of thorns starfish, *i.e. Acanthaster planci*. N/A means the number of trajectories is too high to be analyzed.

two reachabilities were tested: from H12 to H29 and from H12 to H9. The H12–H29 diagnostic was *true* and we obtained 17 possible trajectories. Eight trajectories start with a local bleaching event occurring between the 30th and 90th day of water temperature elevation, four others start with a massive bleaching event occurring between the 30th and 90th day of water temperature elevation, four others begin with an *Acanthaster* outbreak that ends after 60 days, and the last trajectory starts with a hurricane. The 2-year timed test diagnostics are *true* for all those trajectories. However, the model is unable to rank these output. All of them appear equally possible to the analyst.

A large number of trajectories were immediately rejected by the model-checker (*e.g.* Polygons P9, P10, P19). Most of these

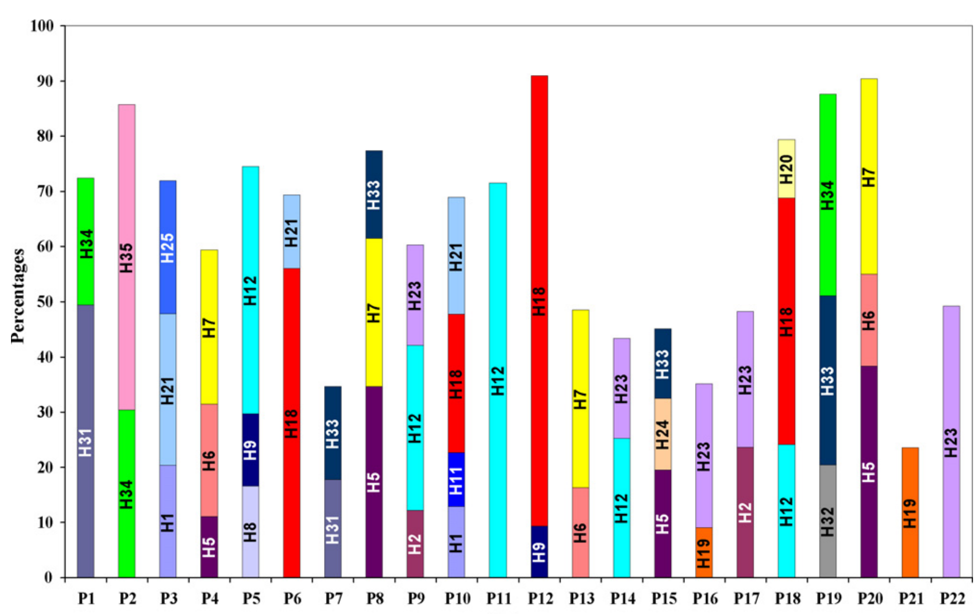

Fig. 11 – Before-hurricane percentage of habitat occurrences in each polygon (P1–P22) according to IKONOS image classification. Labels in the bars refer to the habitat typology described in Table 4.

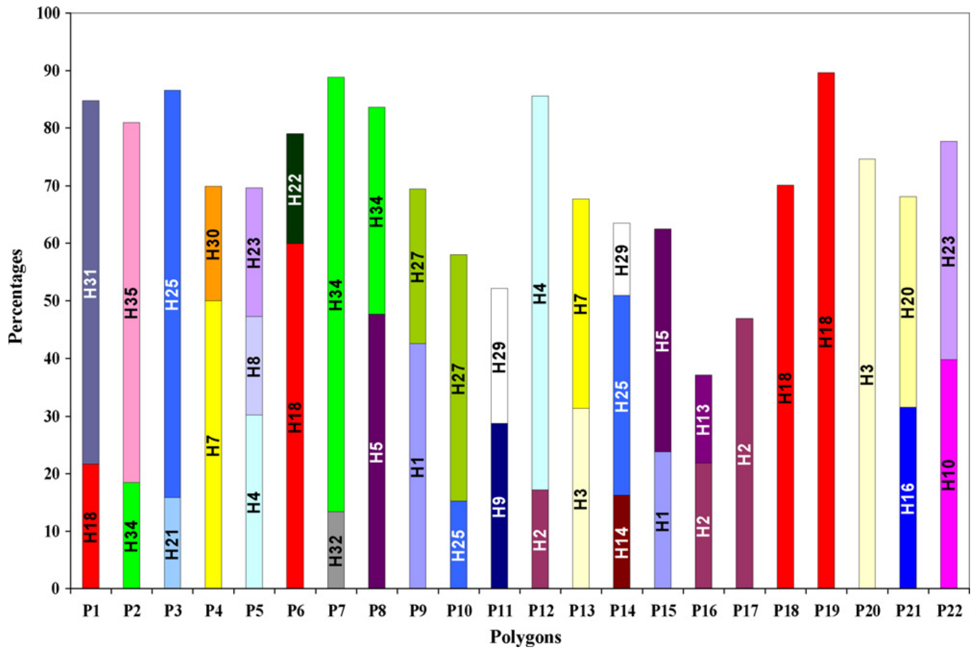

Fig. 12 – After-hurricane percentage of habitat occurrences in each polygon (P1–P22) according to IKONOS image classification. Labels in the bars refer to the habitat typology (Table 4). Differences with Fig. 11 are due to actual changes on the reefs and image classification errors due to high complexity of habitat typology (Table 4). The later are tested with the model (Table 5).

trajectories were not realistic in terms of substratum evolution and strategy-shifts. For instance, all reachability tests from an Open Branching community toward another type of coral community are *False*, since Open Branching automaton was not composed with any other communities. All these discarded trajectories were wrongly suggested by image classification results. For other polygons, several transitions were also *a priori* discarded, but many warranted further model checking (Table 5, columns 1–6).

From the 19 polygons with 75 testable habitat trajectories, we derived a typology of behaviors, and compiled a decision flow chart that summarizes the different cases (Fig. 13). We found that:

- Sixteen trajectories suggested habitat stability, with transition from one state to the same, a virtual transition that the model always declare *true*. Several of these stable transitions occurred for slightly impacted zones and thus were rightly described by image classifications and by the model. However, several of these stable trajectories were in conflict with other possible trajectories that cross radiometrically similar classes. For instance, Polygon P2 suggests either stability (H35–H35, or H34–H34) or increase in coral cover (H34–H35).
- Five realistic transitions were declared non-reachable by the model (*false* diagnostic without time constraints). Interestingly they were real, and visually striking on the images, with new rubble zones covering previous coral zones. These *false* transitions reveal model shortcomings (ecological assumptions and dynamics between transitions) that we discuss in Section 4.
- Thirty transitions were reachable. With clock constraints, 14 transitions were approved by the model, but for 5–15 years intervals (not shown in Table 5), and 5 needed more than 15 years. Most of these trajectories were related to strategy-shifts with transitions to high coral cover. They did not fit in the 2 years time interval bounded by the remote sensing images. Since they were suggested by image classification results, these trajectories point out to image classification errors. One trajectory from habitat H23 to H2 found in Polygons P16 and P17 had too many possible trajectories (>12,000) to be able to take any decision on the local history. Several other tests also provided very high number of trajectories (>400) but this time with a limited number of initial transitions. Eleven trajectories were reachable in 2 years. Polygons that have possible trajectories in 2 years with manageable number of options are P2, P4, P7, P11, P12, P14, P16 and P22.
- Polygons P16 and P22 are both classified as High coral cover compact branching communities. This is true for P22 but not P16, which is a tabular community according to ground-truthing. This error points out to a final pattern, when wrong image classification outputs (either during the before or after classification) can suggest realistic trajectories. This is without any doubts the most difficult source of error to identify if no ground-truth data exists, which will be unfortunately the norm for past time-series of images.

4. Discussion

Modelling exercises that forecast trajectories cannot assess the utility and accuracy of the model since validation data are not available until the necessary time has passed (Wooldridge et al., 2005). Given its documented recent history, Aboré Reef

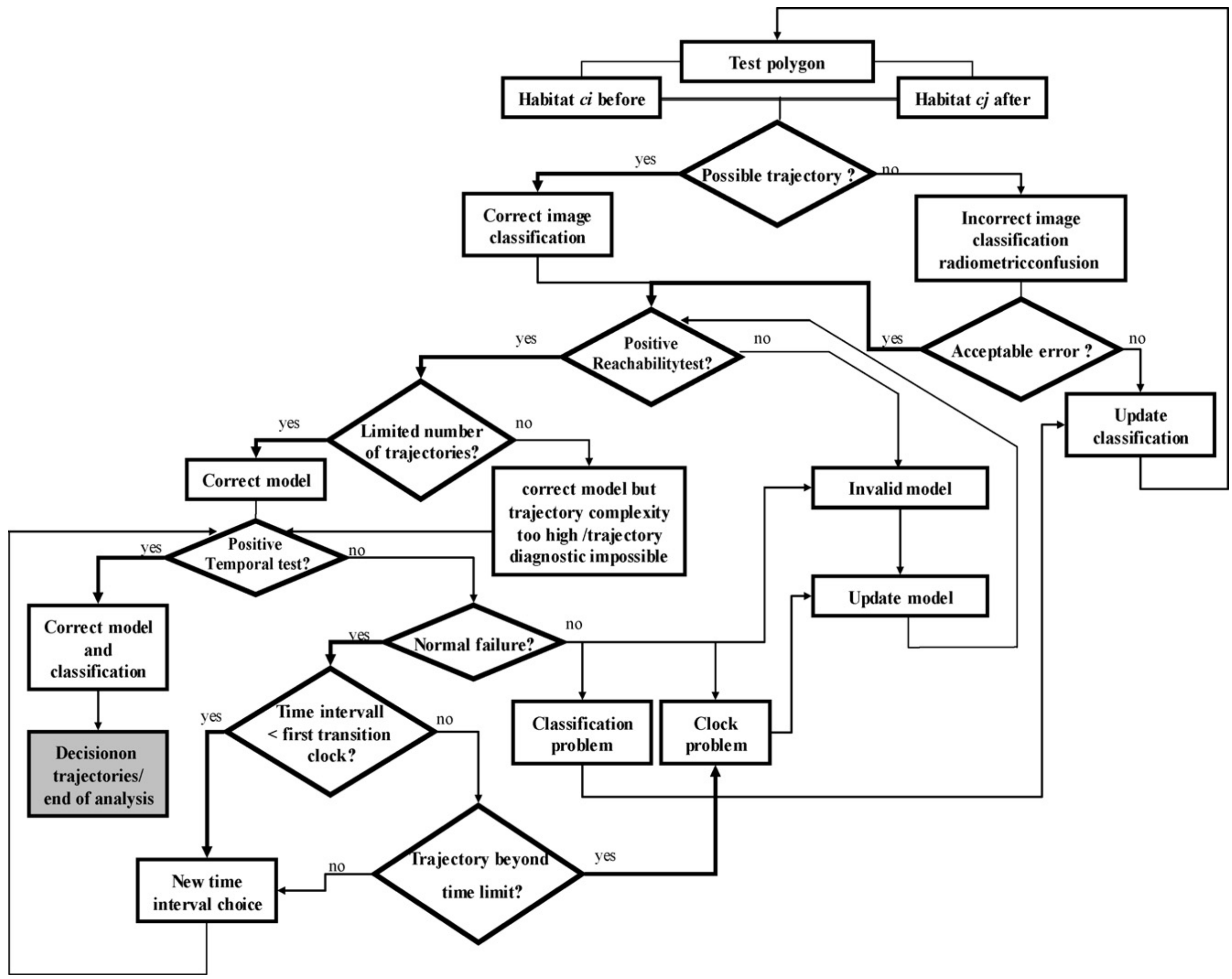

Fig. 13 – Flow chart summarizing the different stages requested for the validation of a trajectory analysis (grey box) when using a timed automata and remote sensing information.

was a useful hindcasting case study to assess the proposed modelling approach.

Thematically, from the polygons that have been correctly classified using the before and after images, we conclude from the model (Table 5) that

- mix coral community from the back reef (*e.g.* Polygon P4) have experienced increase in rubble, and stable or increasing coral cover;
- mix and compact branching communities on reef flats have been damaged by a hurricane (P14 or P11, from a Very High coral cover compact branch community on rocky substratum to a rubble zone with Very Low coral cover and turf). All the different possibilities for P11 called for a hurricane in Year 1 or 2, alone or in combination with coral bleaching or COT predations. With P12, it is suggested that these communities, and other from the back reef have been also impacted by either bleaching or COT outbreaks;
- the open branching communities of the sedimentary accumulations did not suffer from any perturbations and have maintained continuous growth. These are the conclusions for both P2 and P7 Open Branching polygons (Medium to High coral cover for P2, Very Low to Medium for P7).

Since we previously knew all this from field work observations, we did not create new information about Aboré Reef dynamics using the model, but we did uncover the possibilities of using TA and remote sensing from Aboré Reef. At this stage, we still need to be critical of the hypotheses and methods before applying these methods to diagnose a reef with unknown history. We discuss after the pros and cons of this approach.

Methodologically, this study demonstrates that evolution of habitats in coral reef environments can be handled by the timed automata formalism. States, transitions and clocks allow straightforward representation of expert knowledge about what is known of the various events (disturbances and recovery) and their differential impacts on coral habitats and cover. All of these objects can be combined modularly. We have demonstrated that it is possible to infer from a model designed for one given type of reef (Indo-Pacific barrier reef) trajectories of habitat evolution which can be filtered according to time constraints. The model also allowed inclusion of multiple disturbances impacting different types of communities, each with their specific responses. In addition, instantaneous events as well as long-term events (from 1 day to decades) can be considered. The fact that the model works with qualitative intervals enables application to poorly constrained systems, where no continuous data records are available. Expert knowledge can easily be used, and in contrast with Bayesian approaches, there is no need to elaborate probability distributions (sometimes implying significant amounts of field data) to propagate the information. By using a complex habitat typology, with 36 habitat classes, we predictably created spectral confusion using multispectral sensors, many image classification errors and thus suggested a large variety of trajectories, realistic or not. The model did a good job at detecting impossible trajectories, and transitions that requested a much longer time frame (5–15 years). This shows that the model has played its role in detecting image interpretation problems.

Several drawbacks in the timed automata approach balance the positive aspects. The capacity to combine different automata is a great engineering benefit, but it can also be quickly limiting. The Aboré Reef model is close to the maximum level of automata composition that could be handled. Several concessions were made during the implementation process to keep the model manageable (*e.g.* limiting the number of classes of coral cover to five; Table 2). Therefore, models are likely to be bounded by local specificities and will not be useful for a wide range and diversity of reef systems. For instance, a reef with 30% coral cover is fairly rare in the Caribbean (Lang, 2003), but still a common sight in the Indo-Pacific. Thus, digitization of continuous quantitative variables needs to be locally optimized. The fact that only qualitative discrete intervals can be handled implies that model sensitivity depends on the number of these intervals. This was also a problem for the interface with the image since only thematic classes can be handled, and not continuous radiometric intervals (spectral signatures) or habitat continuous gradients. Hybrid models (Alur et al., 1996; Henzinger et al., 1997) combining both possibilities may be more suited for directly using remote sensing quantitative data. Furthermore, it should be even more interesting to inject in these models the capacity to handle properties expressed using fuzzy logic membership functions. Timed automata are interesting because they allow uncertain time constraints, but state properties are also frequently uncertain and continuous by nature. Fuzzy logic capacity has been implemented in cellular automaton models (Liu and Phinn, 2003), and for coral reef habitat mapping (Andréfouët et al., 2000). Thus, it seems appropriate that fuzzy logic formalism can also be included when developing tools that combine models and remote sensing.

The model has made in several cases a *False* diagnostic where it should have been positive. For instance several appearances of rubble, correctly classified by the image, are not validated in 2 years because the model implies that rubbles are locally produced across time, not brought instantaneously from outer areas. This kind of event with inter-habitat spatial relationships is more easily implemented with spatially explicit cellular automata than with timed automata, which are not inter-habitat ruled and spatially explicit, except through the connection with mapped classes of habitats.

5. Conclusion

The Aboré Reef in New Caledonia struck by Hurricane Erika in 2003 provided a well-constrained case study to explore the different aspects of combining remote sensing and the timed automata formalism for ecological trajectory analysis. The before–after high-resolution images provided a variety of trajectories that were tested with the model. We purposefully created unrealistic trajectories, in addition to those observed *in situ*, to assess the behavior of a timed automaton that required significant expert knowledge to be implemented. The conclusions of this study are mixed. We believe after this study that the combination of remote sensing with modelling is definitely a path to follow even for the most difficult configuration (*i.e.* high habitat complexity and multispectral sensors, *versus* for instance moderate complexity and hyperspectral sensors). However, using the timed automata formalism, it is clear that a model must be locally optimized, along with local image interpretation results to refine the diagnostic. A large number of habitats and large time interval lead to high trajectory complexity. Thus, frequent image acquisitions are required to calibrate/validate the model predictions and avoid too many long periods without information.

This study provides a first reference for future use of similar approaches to other sites. These can be areas where no history of *in situ* data are available, but only time-series of images and generic knowledge on communities (recovery rates and so on) which is required to set transitions, states and clocks, can be obtained. At other sites, trophic relationships and other processes (roles of herbivorous fish and invertebrates, over-fishing, coral diseases, pollution, sedimentation, *etc.*) and other communities from other geomorphological zones (forereef, lagoon, fringing reefs) may be required. These will pose new challenges.

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